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Modelling fish colour constancy, and the implications for vision and signalling in water.

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Summary statement. Models of light propagation in water and visual mechanisms show how changes in depth and distance alter visible spectra, and predict the consequences for fish colour vision and colour signals.

SUMMARY

Colour vision and colour signals are important to aquatic animals, but light scattering and absorption by water distorts spectral stimuli. To investigate the performance of colour vision in water, and to suggest how photoreceptor spectral sensitivities and body colours might evolve for visual communication, we model the effects of changes in viewing distance and depth on the appearance of fish colours for three teleosts: a barracuda, *Syphraena helleri*, which is dichromatic, and two damselfishes, *Chromis verater* and *C. hanui*, which are trichromatic. We assume that photoreceptors light-adapt to the background, thereby implementing the von Kries transformation, which can largely account for colour constancy in humans and other animals, including fish. This transformation does not however compensate for light scattering over variable viewing distances, which in less than a metre seriously impairs dichromatic colour vision, and makes judgement of colour saturation unreliable for trichromats. The von Kries transformation does substantially offset colour shifts caused by changing depth, so that from depths of 0 to 30m modelled colour changes (i.e. failures of colour constancy) are sometimes negligible. However, the magnitudes and directions of remaining changes are complex, depending upon the specific spectral sensitivities of the receptors and the reflectance spectra. This predicts that when judgement of colour is important, the spectra of signalling colours and photoreceptor spectral sensitivities should be evolutionarily linked, with the colours dependent on photoreceptor spectral sensitivities, and vice versa.

INTRODUCTION

Fish are known for their bright colours, but how do these colours evolve, and how can they work as signals? It is thought that land animals detect form and motion mostly by luminance, while colour serves object recognition. This is because the pattern of light and shade make it difficult to judge the overall reflectance (grey level) of a surface, whereas the spectral composition of reflected light is a relatively stable cue to material properties (e.g. pigmentation; Rubin and Richards, 1982; Livingstone and Hubel, 1988; Gegenfurtner and Kiper, 2003; Osorio and Vorobyev, 2005; Attewell and Baddeley, 2009). Nonetheless, terrestrial illumination spectra do vary, so that judgement of a reflectance spectrum - known as 'object colour' or 'absolute colour' - requires colour constancy: that is the ability to discount the effects of illumination on colour appearance. Colour vision can therefore be understood as a means to recover reflectance spectra from photoreceptor signals (Barlow, 1982; Buchsbaum and Gottschalk, 1983; Maloney, 1986; Vorobyev and Osorio, 2005).

At short ranges ($<0.1\text{m}$) in shallow water colour vision can operate much as it does on land, but natural waters scatter and absorb light far more than air, which makes colour constancy difficult (Figures 1,2; Jerlov, 1976; Mobley, 1994; Osorio *et al.*, 1997; Johnsen, 2012; Cronin *et al.*, 2014). Vorobyev and others (2001; Marshall and Vorobyev, 2003) modelled colour constancy based on the von Kries transformation (see below), for the red and brown fish *Scarus spinus* and magenta and yellow fish *Pseudochromis paccagnellae*, and concluded that it failed to compensate for changes in the colour with varying distance. Consequently, aquatic animals have been thought to be less concerned with the representation of reflectance spectra (or object colour) than with the detection of visual contrast - either within the coloration pattern itself, or against the background. Notably, the chromatic offset hypothesis proposes that aquatic animals evolve multiple cone classes to enhance the visual contrast of objects seen in open water (McFarland and Munz, 1975; Lythgoe, 1979; Sabbah and Hawryshyn, 2013). Marshall and others (2006) examined the colours used by several fish species as communication signals by comparing visual systems and their performance over depth in various marine light environments. The study did not consider colour constancy, but its conclusion that a fish's pattern could be a more reliable signal than its colour (Marshall *et al.*, 2006), is supported by evidence that cichlid cone sensitivities are well adapted for detecting patterns (Sabbah and Hawryshyn, 2013).

From the foregoing arguments it follows that where colour is used for communication over distances of greater than roughly 0.1m (depending on turbidity) or at varying depths, it is the patterns rather than the colours themselves that are the primary signals (Marshall *et al.*, 2006); a conclusion which contrasts with the emphasis on object colour as the primary signal for land animals (Hill and Montgomerie, 1994; Osorio and Vorobyev, 2008). Nonetheless, object colour is thought to be important to fish communication (Houde, 1997; Seehausen *et al.*, 2008; Elmer *et al.*, 2009; Maan and Sefc, 2013), so one can ask under what conditions it might be used: are some colours expected to offer more reliable signals with variable depth and/or viewing distance than others, and will the best set of receptors be general for all spectra in a given visual environment, or will it depend on the specific reflectance spectra?

Colour constancy in water

Perceptual constancies allow an observer to perceive the cause of a stimulus (e.g. an object), despite variation in the stimulus received by the sense organs. Human colour constancy involves both low level (e.g. retinal) and high (e.g. cortical) level mechanisms (Brainard and Freeman, 1997; Smithson, 2005; Foster, 2011), but it is logical to start with physiologically and mathematically the simplest colour constancy mechanism, namely the von Kries transformation, whereby each photoreceptor's response is normalised to the average for that

receptor class across the image (Eqns 3,4; Worthey and Brill, 1986; Smithson, 2005; Foster, 2011).

The von Kries transformation can, at least formally, be attributed to light adaptation, which takes place in photoreceptors and other early stages of visual processing (Vanleeuwen *et al.*, 2007; Sabbah *et al.*, 2013), and given the universality of light adaptation it is not surprising that all animals tested, including insects, terrestrial vertebrates and fish, have colour constancy (Dorr and Neumeyer, 1997, 2000; Chittka *et al.*, 2014). It is however difficult to identify the specific mechanism; for example, Neumeyer and co-workers (2002) found that goldfish colour constancy is consistent with a von Kries transformation, but there is evidence that guppies' colour constancy improves with experience (Intskirveli *et al.*, 2002), which is indicative of higher-level processes. Also, it has been suggested that the spectral opponent responses of horizontal cells in teleost retinas have a role in colour constancy (Kamermans *et al.*, 1998). As horizontal cells receive multiple, and often colour opponent, receptor inputs their involvement implies a role for interactions between different spectral receptors, which is inconsistent with a von Kries mechanism (Vanleeuwen *et al.*, 2007).

[FIG. 1 ABOUT HERE]

The model

Here we evaluate the potential and limitations of colour vision and colour signalling in water by modelling of the propagation of light in coral reef water to a depth of 30m. We estimate the responses of fish photoreceptors viewing a set of 25 fish reflectance spectra over a range of depths and distances (Figs. 1-3).

To implement the von Kries transformation the model receptor responses are normalised, either to the horizontal space light - that is the background radiance in open water with a horizontal line of sight -, or to an achromatic background. These two idealised backgrounds are fundamentally different because the spectral composition of light from a reflecting surface changes with viewing distance, whereas the light from open water is fixed.

We consider three coral reef teleost fish (Fig. 2): a barracuda, *Syphraena helleri* (Jenkins), which like many open water fish is dichromatic (see Methods), and two damselfishes, *Chromis verater* (Jordan & Metz) and *C. hanui* (Riffbarch). Both damselfishes are trichromatic, but they have markedly different photoreceptor spectral sensitivities, with *C. hanui*'s being more widely separated, and extending into the UV. We do not model tetrachromatic fish vision (Neumeyer, 1992), but we expect this to be qualitatively similar to that for trichromats (Kelber and Osorio, 2010).

Our aim is not to predict any particular optimal system for colour communication - which would require details of the fish's vision, colours, behaviour and visual environment -, but rather to understand the adaptive landscape on which fish colours and colour vision co-evolve (Seehausen *et al.*, 2008; Miyagi *et al.*, 2012). Specifically, to: *i.*) compare trichromacy and dichromacy; *ii.*) examine the effects of varying photoreceptor spectral tuning in trichromats; *iii.*) model how the reflectance spectrum affects colour constancy; and *iv.*) ask whether performance is sensitive to whether the background is open water or a reflective surface.

METHODS

Illumination and viewing conditions

Light scatter and absorption mean that in water the illumination spectrum falling on a surface is dependent on its orientation (Figs. 1,2; Johnsen, 2012). We assume here that the surface being viewed is Lambertian (matte), and oriented perpendicular to a horizontal line of sight. The background is either open water, that is ‘space-light’ (Johnsen, 2012), or a matte spectrally neutral surface (i.e. with equal reflectance across the spectrum) at the same distance as the object; the key difference is that light from a reflecting surface varies with distance, whereas space-light is constant. In fact the reflectance spectra of natural backgrounds, such as sand or coral rubble, are probably not achromatic but tend to increase linearly with wavelength (giving a brownish colour), but any difference would have minimal impact on our conclusions (Osorio *et al.*, 1997).

Aquatic illumination, absorption and scattering (Fig. 2).

[FIG. 2 ABOUT HERE]

Clear tropical coastal waters, such as those of coral reefs, have maximum transmission at about 500 nm (Fig. 2A; Jerlov, 1976). We model spectrally selective scatter by suspended particles following Mobley (1994) and Johnsen (2012). The main optical processes, schematised in Fig. 1, can be formalised by a differential equation (Eqn. 1), which equates the change in horizontal radiance viewing distance with: (1) a positive contribution, denoted S , that describes the amount of light, of wavelength λ , entering the ray, which is predominantly via scattering; and (2) a negative contribution that describes its attenuation (absorption and out-of-ray scattering), proportional to the radiance, which is denoted by a constant α . The horizontal viewing condition makes it possible to treat the medium as uniform along the viewing axis, so S and α do not depend on viewing distance (though they do change with depth). Thus:

$$\frac{d}{dx}L(x) = S - \alpha L(x) \quad [1]$$

where x is the distance from the subject, and $L(x)$ the radiance. Constants α and S were calculated using Hydrolight (Sequoia Scientific) for a Case I bio-optical model, assuming a chlorophyll concentration of 0.5 mg.m^{-3}

Equation 1 can be rewritten in terms of the radiance at the object L_0 (viewing distance of zero) and a “space-light” term L_b , - equal to S/α -, which is the radiance of open water (viewing distance in the infinite limit).

$$L(x) = L_0 e^{-cx} + L_b (1 - e^{-cx}) \quad [2]$$

where $L(x)$ is the radiance at distance x from the object, c is the attenuation coefficient, which equals the sum of the absorption coefficient, α , and the scattering coefficient, S . In this form it is evident that the horizontal radiance is mixture of the reflected radiance and the space-light, weighted by an exponentially decreasing function of distance.

[FIGURE 3 ABOUT HERE]

Photoreceptor responses

We model receptor responses of three teleosts, *Sphyræna helleri*, *Chromis verater*, and *C. hanui* (Fig. 2), which live in or around corals reefs. The fishes’ photoreceptor sensitivities are derived from photopigment absorbances and the transmission of their ocular media (Losey *et al.*, 2003). The 25 reflectance spectra are from freshly captured coral reef fish in Hawaii, which were measured with illumination normal to the surface, and the detector at 45° (Fig. 3; Marshall *et al.*, 2003a).

For modelling receptor responses with light adaptation, photoreceptor quantum catches q_i for each receptor are defined as:

$$q_i = \int_A L(\lambda) r_i(\lambda) d\lambda \quad [3]$$

Where r_i is the rate at which photons activate the photopigment (assuming all photopigment molecules are available for transduction), and A represents the wavelength range over which the integral is performed, in this case 300 to 700nm.

The responses are transformed to a von Kries adapted value, v_i , by division by the quantum catch from the adapting background radiance b_i .

$$v_i = q_i/b_i \quad [4]$$

The transformed values are converted into normalised chromaticity coordinates, n_i , by division by total photoreceptor quantum catch.

$$n_i = v_i/\sum_i v_i \quad [5]$$

These two steps normalise the response relative to the background radiance.

We then assume that receptor responses are compared by opponent mechanisms to give chromatic signals (Kelber *et al.*, 2003). Normalisation of these signals (discounting overall intensity) allows us to represent the dichromat's chromatic signal by the formula:

$$X = (L - S)/(L + S), \quad [6]$$

and to project the trichromatic space in a two dimensional chromaticity diagram (Maxwell's triangle). The projection gives two chromaticity values by a linear transform, namely:

$$X = \frac{\sqrt{2}}{2}(n_1 - n_3) = \frac{\sqrt{2}}{2}(L - S) \quad [7]$$

$$Y = \sqrt{\frac{2}{3}}(n_2 - (n_1 + n_3)/2) = \sqrt{\frac{2}{3}}(M - (L + S)/2) \quad [8]$$

with n_i being ordered by the wavelength of peak sensitivity (λ_{\max}) from short to long. L , M and S refer to the responses of the long, medium and short wavelength sensitive photoreceptor responses respectively (Fig. 2), either before or after normalization to the background (Eq. 4). Note that although scattered light in clear water generally looks blue to divers, and objects become bluer with increasing distance, it is implicit in our model that object colours would move to the achromatic point with increasing distance.

Modelling discrimination thresholds

A failure of colour constancy can be behaviourally significant only if the shift exceeds the colour discrimination threshold, or one just-noticeable difference (JND; here 1-JND will be detected 75% of the time from 2 alternatives). We consider only chromatic signals (i.e. changes in hue and saturation), and assume that colour thresholds are independent of light intensity (i.e. Weber's law holds; Kelber *et al.*, 2003), with receptor noise equivalent to a contrast of 0.05 in each cone type (Figs. 4,6,7; Equations 3,4 in Vorobyev and Osorio, 1998). This estimate of the JND is similar to a recent estimate for a bird (Olsson *et al.*, 2015), although in reality the effects of the ambient illumination – which changes with depth - on receptor photon catch are likely to affect the discrimination thresholds (Marshall and Vorobyev, 2003).

Notes on terminology

The terms hue, saturation and brightness refer to aspects of human colour perception (Wyszecki and Stiles, 1982), which cannot at present be defined for any animal (Kelber & Osorio 2010). Here we use geometric definitions that parallel the human terms. We decompose the space into a brightness axis, and an $n-1$ dimensional chromaticity space. The location in a chromaticity space is given by dividing the receptor catch coordinates by the sum of receptor values

(nominally brightness). Saturation is the distance from the centre of the chromaticity space, and hue is the remaining dimension(s). It follows that a dichromat does not distinguish hue, a trichromat has one dimension of hue, and a tetrachromat two. Note also that the *n*-chromacy (di, tri etc.) is defined not by the number of spectrally distinct cone photoreceptors in the eye but the number of primaries needed to match any colour. Here, in the absence of direct behavioural evidence, we assume that the *Syphraena helleri* is a dichromat, and the *Chromis* species are trichromats.

RESULTS

We model photoreceptor responses of three fish, a dichromat, the barracuda *S. helleri* (Figs. 2,4), and two trichromats, the damselfishes *Chromis hanui* and *C. verater*. (Figs. 2, 5-7), to fish reflectance spectra (Fig. 3) in coral reef water. The models predict how varying the viewing distance, depth and background (Fig. 1) will affect receptor responses and chromatic signals after photoreceptor adaptation to the background (Eqns. 3,4). Modelled colours are plotted in chromaticity diagrams, which represent the colour based on photoreceptor quantum catches (Eqns 3-5, 7,8), in terms of the chromatic aspects of colour (i.e. hue and saturation for humans; Wyszecki and Stiles, 1982), independent of intensity (or brightness). A dichromat has a single chromatic dimension, so colours are represented on a line (Fig. 4), whereas trichromats have two dimensions, which are represented by a plane (Figs. 5-7).

Variation in distance (Figs. 4A, 5)

[FIGURES 4,5 ABOUT HERE]

We modelled the effects of varying viewing distance from 0 – 100m against open water, and a spectrally neutral reflector at the same distance as the object. Visibility falls rapidly, so 100m is in effect infinity (Figs. 4,5; Loew and Lythgoe, 1975; Cronin *et al.*, 2014). Light scatter and absorption (Fig. 1) cause colours to become less saturated with increasing distance, shifting them towards the achromatic point (Figs. 4, 5), which is by definition the background colour. For the trichromatic *Chromis* species spectrally selective absorption has a slight effect, causing hue shifts, which are seen as ‘hooks’ on the plots in the chromaticity diagram (Fig. 5), evident at ranges exceeding 3m.

An open water background does not change with viewing distance, so that the photoreceptors’ adaptation state is fixed, and von Kries colour constancy can have no effect. By comparison, a reflecting background in the same plane as the object changes with distance in a similar manner to the object, which does allow the von Kries transform to take effect. However the transform corrects for multiplicative effects (that is effects of illumination or absorption in most real-world cases), which do not apply to scattering, and in fact the modelled colour changes for the open water and solid backgrounds are qualitatively similar, with colours moving toward the achromatic point (Figs. 4A, 5). Thus the model implies that receptor adaptation to the background will not affect colour changes caused by varying viewing distance, because scatter dominates light absorption by water (Figs. 1,2).

Variation in depth (Figs. 4B, 6-8)

[FIGS. 6,7 ABOUT HERE]

We modelled receptor responses of the three fish species for depths of 0m-30m (Fig. 2), with a viewing distance of 0.3m. Here photoreceptor adaptation substantially offsets the effects of changing depth on the relative rates of photon absorption by the different spectral receptors (Figs. 4B, 6, 7). Nonetheless residual changes (Figs. 4B, 7, 8) may exceed the colour discrimination threshold, and so might cause failures of colour constancy.

[FIG. 8 ABOUT HERE]

For the dichromat, *Syphrena*, which has one chromatic dimension, all the residual changes are towards the achromatic point with increasing depth, but they vary in magnitude for different spectra (Fig. 4B), ranging from <1 to >3 JND's. The larger shifts are for spectra that reflect strongly at long wavelengths, which lie to the right of the neutral point.

For the trichromatic *Chromis* species, residual shifts vary substantially in their magnitudes, and their directions in colour space (Figs. 7, 8). For *C. hanui* the shifts range from 0.005 to 0.05, with a mean of 0.025 units, in the XY colour space, while for *C. verater* shifts are smaller, ranging from 0.005 to 0.04, with a mean of 0.015 units. These values can be compared to the JND, which ranges from 0.01 to 0.02 units, depending on location and direction in the colour space (Figs. 6, 7). The difference between the two species is probably due mainly to *C. verater*'s photoreceptor spectral sensitivities being more closely spaced than *C. hanui*'s, but the particular spectral locations of the receptors is also relevant (Fig. 2; Worthey and Brill, 1986; Osorio *et al.*, 1997), and it is evident that the direction and magnitude of shifts depend upon the specific set of photoreceptors, the spectra and the viewing conditions (illumination spectrum and adapting background). Also, there are examples of metamerism where different spectra have the same colours, for instance spectra 15 and 16 are almost identical for *Chromis hanui*, but not for *C. verater* (Figs 3,7).

DISCUSSION

To examine how absorption and scattering of light might affect colour vision and communication in water (Fig. 1), we modelled chromatic signals for three species of fish viewing fish reflectance spectra. There are four scenarios: either the distance from the viewer to the object varies at a fixed depth (Figs. 4A, 5), or the depth varies at a fixed distance (Figs. 4B, 6, 7, 8), and the background is either open water or a grey surface at the same location as the object. We assume that colour constancy is provided by normalisation of receptor responses to the background (Smithson, 2005; Foster, 2011; Neumeyer *et al.*, 2002). Fish may have additional retinal (Kamermans *et al.*, 1998, Vanleeuwin *et al.*, 2007), and higher level mechanisms (Intskirveli *et al.*, 2002; Smithson, 2005; Foster, 2011), but is it logical to start with von Kries constancy.

Variation in viewing distance

As the distance to the object changes, scatter and absorption remove light, and light is scattered into the path. Scatter is fairly spectrally neutral, but the absorption is spectrally selective, removing long and short wavelengths and leaving blue light (Fig. 1), which is then the light available to be scattered into the path. This moves the spectrum towards that of the open water so that the visibility of the fish declines to near zero over a few meters (Figs, 4A, 5). Furthermore, because an open water background has a fixed spectrum (Figs. 1, 4, 5) colour constancy based on adaptation to the background is useless. When the background is a surface at the same distance as the object von Kries constancy could theoretically have an effect, but in fact, due to the effects of scattered light, the modelled changes of colour are almost identical for open water and reflective backgrounds, with spectral loci moving toward the achromatic point as distance increases (Figs. 4A, 5).

The model implies that the failure of colour constancy with varying distance could not be corrected unless the viewer took account of both the distance to the object and the turbidity of the water, which is probably difficult (but see Schechner *et al.*, 2003). These observations lead to two conclusions: firstly, that for trichromats an object's hue will be more constant than its saturation, and secondly that the range over which a colour can be detected will increase with

increasing saturation (relative to the background). These considerations could account for the intense colours of some aquatic animals. Furthermore, at least for dichromats, like *Syphraena helleri* (Losey *et al.*, 2003), which cannot distinguish hue from saturation (see Methods), this conclusion is consistent with the view that colour vision is concerned more with pattern recognition than object colour (Munz and MacFarland, 1973; Marshall *et al.*, 2006; Sabbah and Hawryshyn, 2013).

Variation in depth

[FIGURE 8 ABOUT HERE]

With varying depth, but fixed viewing distance, spectrally selective light attenuation by water alters colours. In the absence of receptor adaptation - or some equivalent colour constancy mechanism - all colours shift towards the illuminant locus with increasing depth (Fig. 6), but as on land (Smithson, 2005; Foster, 2011), the von Kries transformation would be effective, so that a fish viewing an object from a fixed distance can achieve useful colour constancy over a range of depths: sometimes, over tens of meters, the residual shifts – which correspond to failures of colour constancy - are negligible, falling below the discrimination threshold (Figs. 4B, 7, 8). As expected from theory (Worthey and Brill, 1986; Osorio *et al.*, 1997) the more widely separated receptors of *C. hanui* suffer shifts averaging 40% larger than *C. verater*. In theory, higher level mechanisms might compensate for such failures, but the fact that the residual shifts vary in magnitude and direction (Figs. 7, 8) would complicate any such compensation.

Assuming that accurate judgement of colour over depth is relevant, what are the consequences of the evolution and co-evolution of fish photoreceptor spectral sensitivities and reflectance spectra? It is notable that colour changes for different spectra vary both in their magnitudes and in their directions in the trichromatic colour spaces (Figs. 3, 7, 8). Many spectra shift towards the short wavelength (Lower left) corner of the colour triangle, but blue spectra (e.g. spectra 8, 9 and 10) shift towards the long wavelength corner (Lower right). Similarly, the magnitudes of shifts in the trichromats' colour spaces are not easily predictable, either from the location of the colours in their chromaticity diagrams (Figs. 7, 8), or from their grouping identified by the *k*-means clustering algorithm (Figs. 3, 8): the largest shifts tend to be for spectra with high reflectance at longer wavelengths, such as those in Group V, and the smallest shifts being for those such as Group III with high reflectance at short wavelengths, but there is much variation between related spectra, especially for the reddish colours in group I. Moreover, shifts can be different for spectra that have similar colour loci: for example, for *S. helleri* spectra 6 and 11 (Fig. 4B), and for *C. hanui* spectra 11 and 12 (Fig. 7B); the latter difference probably arises because spectrum 12 is double peaked (Fig. 3). The unpredictability of these colour changes implies that it would be difficult to apply a simple rule to compensate for them, and that the stability of the colour of a given spectrum is contingent upon the local visual environment, and the receiver's colour vision.

Colour and communication in water

Communication depends on a receiver being able to discriminate different possible states of the signaller. Much work implies that object colour is important for fish communication, as it is on land (see Introduction; Osorio and Vorobyev, 2008), but the widespread occurrence of dichromacy in coral reef fish, coupled with recognition of the problem of colour constancy (Marshall *et al.*, 2003b; Marshall and Vorobyev, 2003) suggests that this view may be simplistic. Instead it is argued that receptor sensitivities evolve to benefit contrast with the background, as proposed by the offset hypothesis (Loew and Lythgoe, 1973; Sabbah and

Hawryshyn, 2013), and likewise that the displays of reef fish are adapted to produce conspicuous body patterns (Marshall *et al.*, 2003b).

Despite the problems faced by colour vision in water, we find that at least for trichromatic fish (and by implication for tetrachromatic species), colour constancy can effectively limit colour shifts associated spectral absorption of light at varying depths, but not light scattering with varying distance. It follows that if the level of pigmentation, which typically affects saturation, is an informative component of a colour signal (Milinski and Bakker, 1990; Hill and Montgomerie, 1994) decisions about object colour, for instance in mate choice, even in clear water should be made at fixed ranges of less than 1m. Similarly it follows that for colour variation in saturation, but not so much in hue, the opposite sex always looks better when closer distance, thus fish gain from coming closer! While signals are really only honestly compared if they originate from the same distance.

Trichromats can separate hue from saturation, and hue is little affected by veiling light (Fig. 5). Taking account of both scattering and absorption this implies that the best colours for signalling in water should be saturated, with minimal hue shift following receptor adaptation to the background. Hue changes would then be robust, and potentially informative. In general von Kries colour constancy favours small photoreceptor separations (Figs. 2,7,8; Osorio *et al.*, 1997), but beyond this both the magnitudes and the directions of changes are variable being dependent upon interactions between the photoreceptor spectral sensitivities, reflectance spectra and the visual environment. For example, in clear costal seawater for *Chromis verater*, with its closely spaced photoreceptor spectral sensitivities, many of the bluish spectra would be satisfactory, (Figs. 2,3,7,8). By comparison the larger spectral separation of *C. hanui*'s photoreceptors increase chromatic signals (Figs. 5.7), but this advantage may be negated by failure of colour constancy (Figs., 7,8; and also by reduced quantum catch). Saturated colours, such as 4, 15 and 18, where constancy failures with depth cause shifts in saturation would potentially be useful, because their hue can offer a reliable signal, while colour 23, which has substantial hue shift would be less good.

Our prediction that there will be co-evolutionary interactions between the spectral sensitivities of photoreceptors used for colour vision by aquatic animals and the signalling colours directed at them (Osorio and Vorobyev, 2008; Cheney *et al.*, 2009; Cheney and Marshall, 2009; Hofman *et al.*, 2009) contrasts with the sensitivity hypotheses, which proposes that fish photoreceptor spectral sensitivities tend to match the ambient illumination spectrum (Lythgoe, 1979; Bowmaker *et al.*, 1994). It may therefore be worthwhile to take account of how colour constancy might affect the evolution and co-evolution of fish colours and of photoreceptor spectral sensitivities (Seehausen *et al.*, 2008; Miyagi *et al.*, 2012; Maan and Sefc, 2013).

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COMPETING INTERESTS

None of the authors has any completing interest.

AUTHOR CONTRIBUTIONS

DO, LW and NJM conceived the study, LW and SJ did the modelling. All authors contributed to writing the paper.

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FIGURE LEGENDS

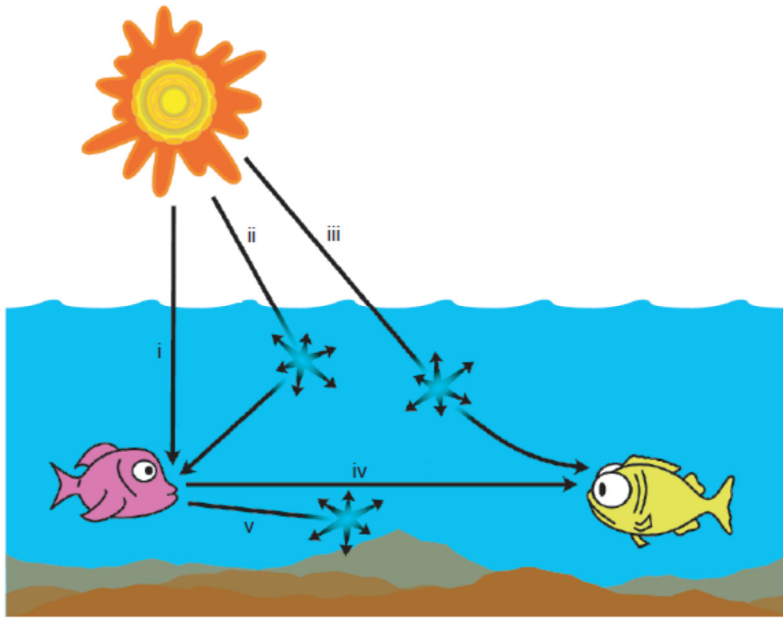


Figure 1. The visual scene.

The object fish (purple) is illuminated directly from above (i) via both single and multiple scattering events in the water (ii). The observer (green) is at the same depth. Light reaching the observer from the direction of the stimulus is a combination of light scattered by the water (iii) and light reflected from the stimulus (iv). Light reflected by the stimulus is lost through scattering and absorption (v). We model the object viewed against a background, which is either horizontal space light, that is the light seen in open water, or a surface reflecting equally at all wavelengths (not illustrated). Note that light reaching the eye from the achromatic background changes with the viewing distance of the object, whereas the open water background is fixed.

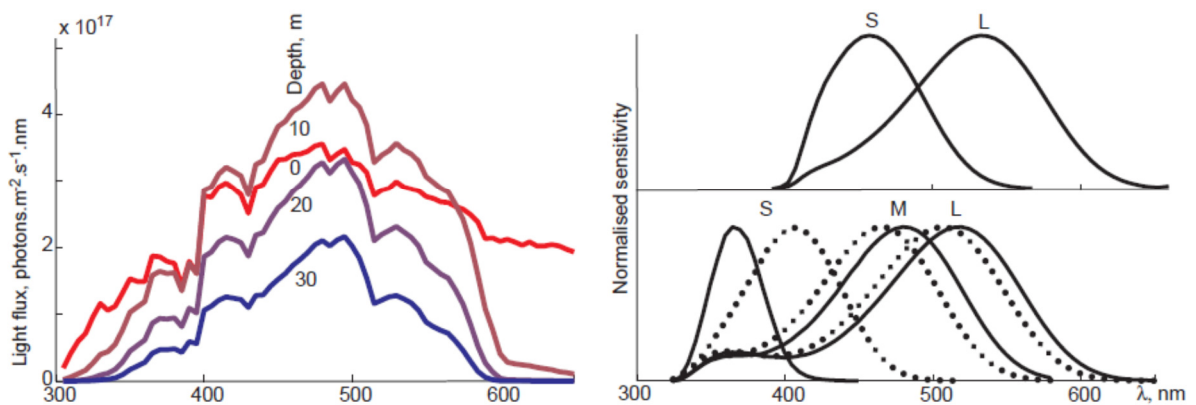


Figure 2. Illumination spectra and photoreceptor spectral sensitivities.

Left: Modelled illumination spectra in coral reef water at depths of 0, 10, 20 and 30m (see Methods). Note that the light flux at 10m exceeds that at the surface in the 450-500nm range, this is due to scattered light, and is dependent on the orientation of the stimulus relative to the surface. *Right:* Spectral sensitivities of the fish photoreceptors used in our models. *Upper Panel:* Barracuda *Sphyræna helleri* a dichromat; *Lower Panel:* Trichromats, *Chromis hanui* (solid lines) and *C. verater* (dotted lines).

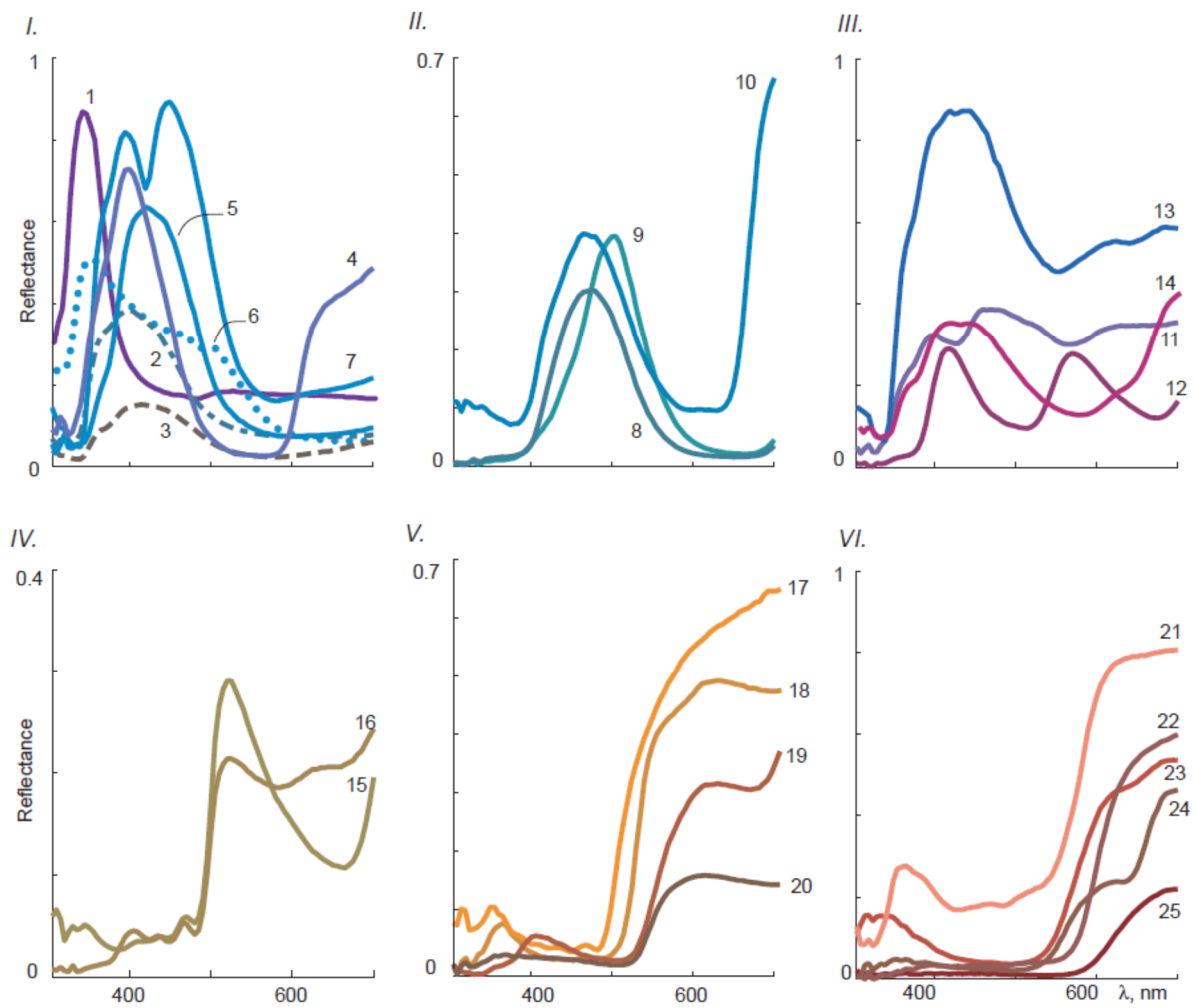


Figure 3. Fish reflectance spectra.

Twenty-five reflectance spectra from coral reef fish (Losey *et al.*, 2003) used for the models. The line colours are given by the CIE loci of the spectra, and so approximate their appearance to a human. To identify natural categories of spectra (as opposed to classifications based on visual responses) they are placed into six groups (I – VI) by normalising them to their respective maxima, square-root transformation (to reduce effects of overall reflectance) and then classifying them with the Matlab (Version 2012a) *k*-means clustering algorithm, using the ‘correlation’ parameter. This classification is a convenient way to group the colours according to their *reflectance spectra*, as opposed to photoreceptor excitations, and it is interesting to note how they cluster and shift in the fish colour spaces (Figs. 4,5,7,8).

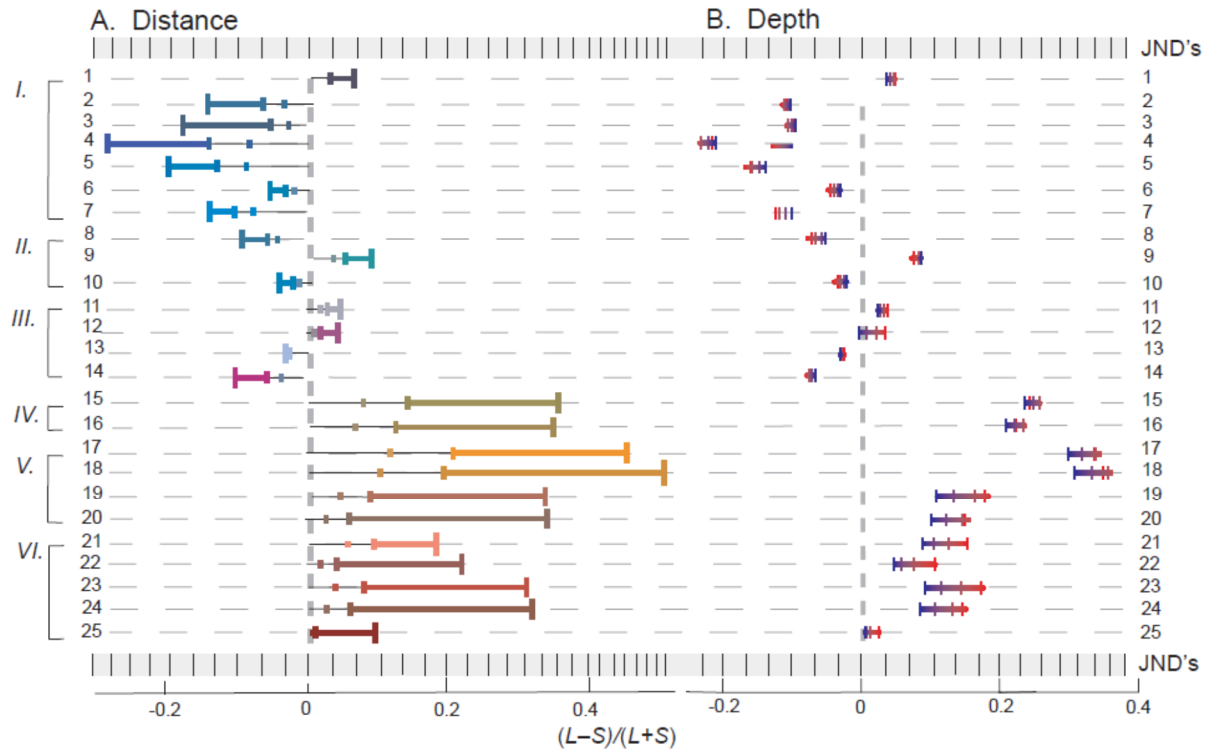


Figure 4. Colour shifts for the dichromat *S. helleri* as a function of depth and distance.

Plots show modelled shifts of fish spectra (Fig. 3). A.) with distance at 2m depth against an achromatic background, tickmarks show the chromatic signal at 0, 1 and 2m, the first metre is coloured as in Figure 3; and B.) with depth from 0m to 30m at a distance of 0.3m (c.f. Figs. 5,7), tickmarks indicate 10m intervals, coloured from red to blue with increasing depth. It is assumed that photoreceptors are adapted to the achromatic background (Fig. 1). The origin corresponds to the achromatic point. Numbers along the left and right margins identify the spectra, arranged in the six groups identified in figure 3, and the scale along the upper and lower margins indicates the just noticeable differences for the chromatic signal assuming a Weber fraction of 0.05 in both cone types.

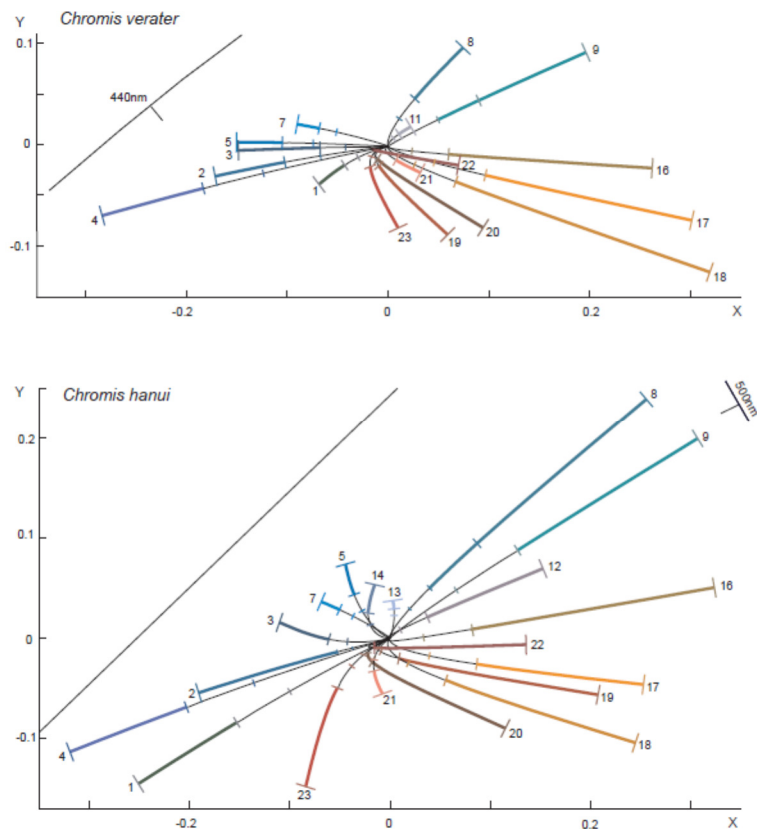


Figure 5. Colour shifts for trichromats with varying viewing distance.

The fish spectra (Fig. 3) viewed at varying distance at 2m depth from 0 to 100m (effectively infinity) with von Kries normalisation of modelled receptor responses to an achromatic background. Tickmarks show the chromatic signal at 1m intervals, with the first metre coloured as in figure 3. Plots are receptor based chromaticity diagrams for *C. verater* and *C. hanui*, which represent the colours on a plane of equal brightness (Fig. 6; Eqns 3-5, 7, 8). With increasing distance the predominant shift is a decrease in saturation, with colours moving towards the achromatic point (i.e. the origin), due to scattered light. Minor hue shifts are apparent in the curvature of the lines, and the variable ‘hooks’ seen at long ranges. The effects are very similar for an open-water background and at greater depths.

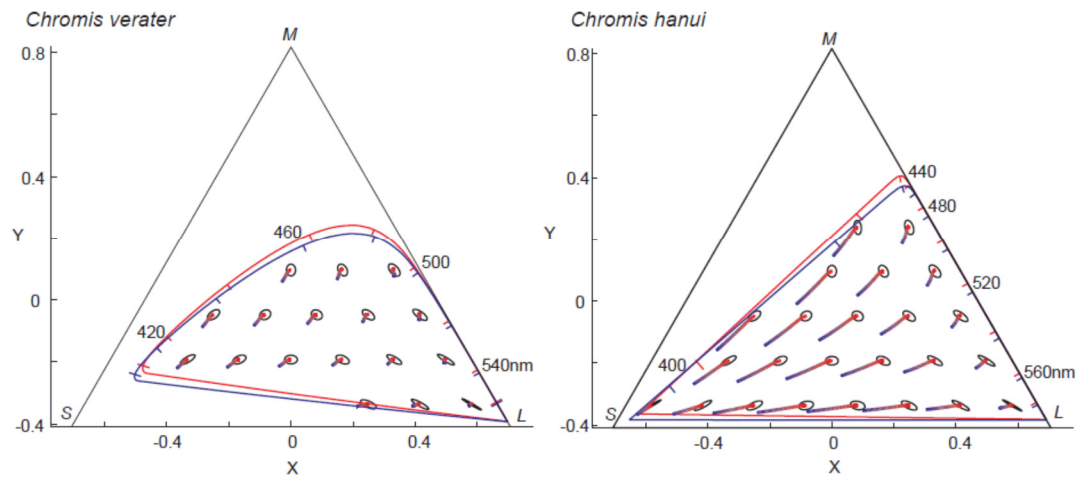


Figure 6. Shifts of trichromatic colour loci due to photoreceptor adaptation at depths from 0m to 30m (lines) and colour discrimination thresholds (ellipses).

The lines show the *correction* imposed by receptor adaptation for a depth range of 0-30m (red: shallow, blue: deep) for *Chromis verater* (A) and *C. hanui* (B) adapted to horizontal space light. The magnitudes of the transformation vary across the colour space. Differences between the two species are related to the differences in receptor sensitivities (Fig. 2). Corrections are dependent on the chromatic locus; they are smallest for spectra that excite single photoreceptors and largest for those that excite both L and M receptors. *C. hanui* has larger corrections than *C. verater* probably due to the greater spectral separation of the photoreceptors. Ellipses show approximate colour discrimination thresholds estimated assuming that receptor noise limits performance with a Weber fraction of 0.05 in all three cones (Vorobyev and Osorio, 1998). The boundary lines plot the monochromatic loci for depths 0m and 30m. Shifts produced by adaptation to an achromatic background are similar.

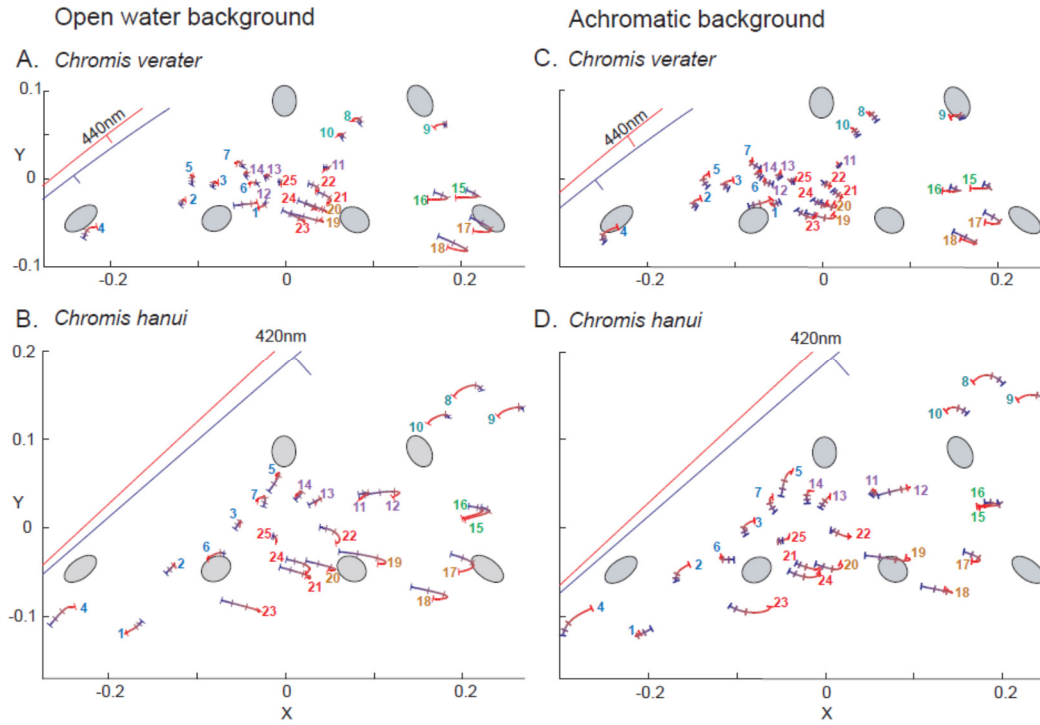


Figure 7. Colour shifts for trichromats after correction by the von Kries transformation.

Shifts of loci in the colour spaces of *C. verater* and *C. hanui* to the fish spectra (Fig. 3) after receptor adaptation to background radiance from 0m (red) to 30m depth (blue), with tickmarks at 10m intervals, for horizontal space light and achromatic backgrounds. The axes and plotting conventions are for figures 4B, 5 and 6. The residual changes vary substantially in magnitude and direction. Grey ellipses are the 1-JND values as plotted in Fig. 6. Numbers identify the spectra as given in figure 3, and are coloured schematically according to their group (I-VI) in that figure.

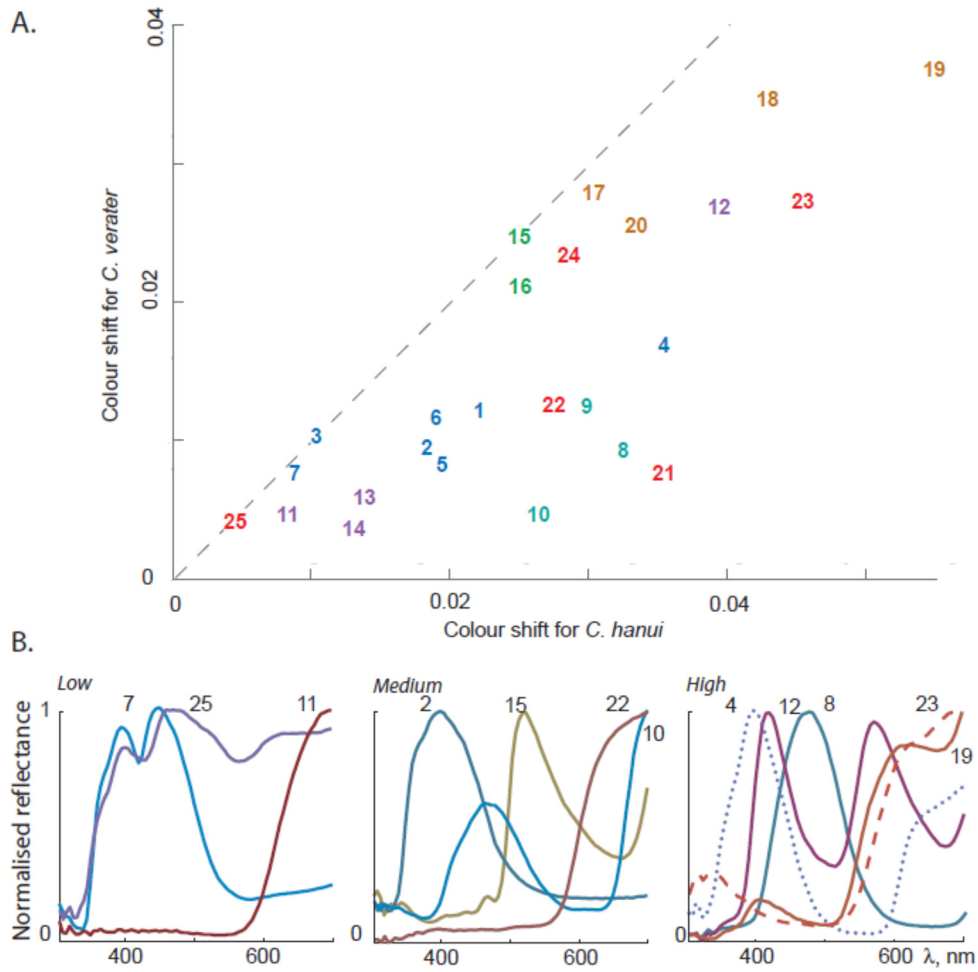


Figure 8. Colour shifts due to colour constancy failure differ between the two *Chromis* species and between related spectra.

A.) Modelled colour shifts experienced between 0 and 30m. Shifts are maximum displacements over the depth range 0 – 30m for an open water background (Fig. 7). The mean shifts for *C. verater* and *C. hanui* 0.0152 and 0.0256 respectively, and the correlation coefficient between shifts is 0.78. A JND is approximately 0.01 – 0.02 units (Fig. 7). Numbers identify the spectra as given in figure 3, and are coloured schematically according to their group (I–VI). B.) Examples of spectra giving low (<0.015), medium (0.015 – 0.03) and high (>0.03) shifts for *C. hanui*. One of each of the spectra from the classes I–VI (Fig. 3) that fall into the relevant range is illustrated. The spectra are normalised, and numbered as in Figure 3.